



Molluscan assemblages associated with intertidal vermetid formations: a morpho-functional approach

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KEY WORDS: intertidal, vermetid formations, mollusc, Sicily, Mediterranean.

ABSTRACT Vermetid platforms are peculiar bioconstructions stretching along the calcareous shores of western Sicily where they appear as a rocky framework at the intertidal level. A survey of their gastropod fauna was carried out based on their shell morphology and the feeding role of each species. The results further substantiate our previous hypothesis referring to the vermetid platform as a horizontal extension of the spatial niches of the most significant infralittoral taxa. Species distribution along a multifactorial gradient is also indicated. Two major dimensions characterize the spacing of the biotic components: one refers to the sea-land axis; the second is related to the height of the structure above mean sea level.

RIASSUNTO L'approccio morfo-funzionale allo studio del popolamento a Molluschi associato alle formazioni a vermeti. La malacofauna di una biostruttura a vermeti della Sicilia nord-occidentale è stata esaminata utilizzando alcuni descrittori morfologici e funzionali, basati sui parametri conchigliari e sulle caratteristiche trofiche delle specie. I risultati, ottenuti utilizzando i soli Gasteropodi conchigliati, hanno consentito di confermare il ruolo ecologico del "trottoir" a vermeti, inteso come dilatazione della nicchia spaziale di molte specie, soprattutto infralittorali. In secondo luogo di leggere in maniera molto più dettagliata la distribuzione delle specie lungo l'ipotetico gradiente multifattoriale che regola la comunità, disposto sia secondo la direzione costa-mare sia secondo l'altezza della struttura sul livello medio del mare. I morfogruppi "leggono" questo doppio gradiente e si dispongono lungo la piattaforma in relazione ad esso.

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INTRODUCTION

"Trottoir à vermetes" (PÉRÈS & PICARD, 1952) are biogenic constructions (*sensu* LABOREL, 1987) formed by the species *Dendropoma petraeum* (MONTEROSATO, 1884) and are typical of the rocky coasts the northwestern Sicily. They are flat horizontal reefs lining most rocky calcareous shores in the southern Mediterranean where they make up a highly indented structure.

They grow perpendicular to the coastline, from land to sea, forming true "récif-barrière" in which a well-developed community is found (CHEMELLO, 1989; MANNINO, 1992; ORLANDO, 1978; PANDOLFO *et al.*, 1992a, 1992b; SAFRIEL & BEN-ELIAHU, 1991). Vermetid platforms were first reported on the rocky shores of Isola delle Femmine (northwestern Sicily) (QUATRE-FAGES, 1842; PÉRÈS & PICARD, 1952; MOLINIER & PICARD, 1953) and are documented to inhabit the rocky coasts of temperate and tropical seas (KEEN, 1961). With the isolated exceptions of the Caribbean Sea (JONES & HUNTER, 1995) and the Island of Fernando de Noroña in Brazil (KEMPF & LABOREL, 1968), the most important constructions are found in the Mediterranean sea. Apart from in Sicily, vermetid platforms are present along the coasts of Israel (SAFRIEL, 1966; 1974; 1975) and Lebanon (DALONGEVILLE, 1977; BITAR & BITAR-KOULI, 1995a; 1995b), southern Turkey (LABOREL, 1987), Crete (KELLETAT, 1979; LABOREL, 1987), Malta (AZZOPARDI, 1992), Algeria (MOLINIER & PICARD, 1953), Corsica (MOLINIER, 1955a; 1955b) and Spain (TEMPLADO *et al.*, 1992).

The "trottoirs" of NW Sicily are by no means simple structures, but are complex systems which share the major features of mid- and infralittoral levels and include many habitats subject-

ed to diverse environmental conditions. A typical vermetid platform can be divided into a number of different zones (CHEMELLO, 1989): a- *Lythobipillum lichenoides* cushions, the biological marker of the inner margin of the vermetid platform; b- one or more "cuvettes", little pools which remain covered by sea water and separated from each other by small vermetid crests; c- an elevated outer margin; d- the upper infralittoral fringe. Level is characterized by a "facies" of the Phaeophyceae *Cystoseira amentacea* var. *amentacea* (GIACONE & DE LEO, 1966).

Information on the malacofauna of Sicilian platforms is restricted to a few taxonomic reviews (ORLANDO, 1978; PANDOLFO *et al.*, 1992a), dimensional analyses of the "trottoir" (BADALAMENTI *et al.*, 1992a; 1992b; CHEMELLO, 1989) and descriptions of the assemblage structure (CHEMELLO *et al.*, 1990; PANDOLFO *et al.*, 1992b) while the relationships between habitat complexity and associated polychaete communities have been indicated only for formations in Israel (SAFRIEL & BEN-ELIAHU, 1991).

Attempts to propose simple developmental models of the "ecological functioning" of vermetid bioconstructions and to trace significant relationships between gastropod growth and the abiotic environment have been frustrated by the high degree of complexity of the ecosystem. Water movement and turbulence through the platform are the main physical factors affecting the vermetid constructions. Their high variability and chaotic growth make assessment difficult and rather unreliable.

Our attempt to overcome this constraint has led to the use of appropriate biological descriptors, based on the supposed corre-

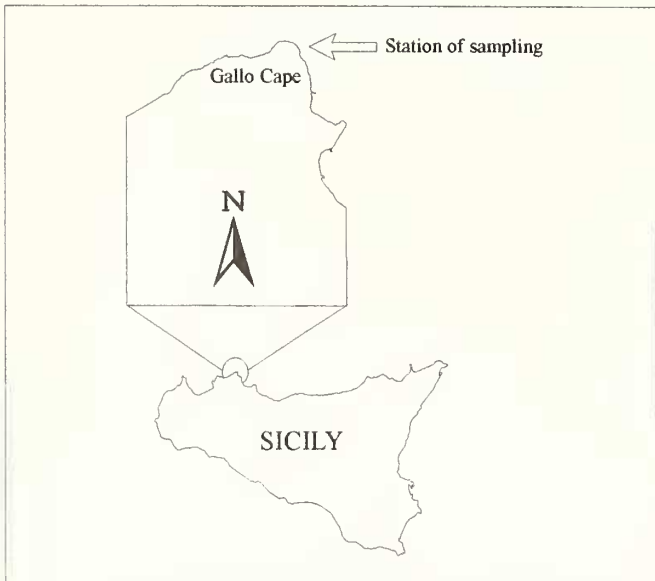


Figure 1. Gallo Cape (Northwestern Sicily): station of sampling.

spondence between the morphology of shelled gastropod molluscs and the structure of their settlements under the influence of the main abiotic factors. A number of morpho-functional parameters have been chosen, which have already been tested in other molluscan communities (RUSSO 1986; RUSSO, 1989). Our survey has resulted in a thorough analysis of the effects of hydrodynamism on the distribution of shelled gastropods along a short environmental gradient. The result is significant despite the fact that non-shelled and non-fit molluscan species were not included in the analysis. Bivalves, polyplacophorans and non-shelled gastropods are therefore not taken into consideration, although they play an important role in the structuring of the malacocoenosis (PANDOLFO *et al.*, 1992b).

MATERIALS AND METHODS

Eight square samples (400 cm² in area) were scraped from the surface of the biogenic platform using a hammer and chisel in March 1994. The study site was Cape Gallo, at the westernmost limit of the Gulf of Palermo (NW Sicily) (Fig. 1). Samples were collected from the following zones and biogenic facies characterizing the platform (Fig. 2): 1 - *Lithophyllum lichenoides* (LIT) cushions; 2 - inner border (BI) formed by a thin vermerid layer; 3 - first cuvette (CV1); 4 - second cuvette (CV2); 5 - *Dendropoma petraeum* (CR) crest; 6 - third and deepest cuvette (CV3); 7 - outer border (BE) formed by a thick vermerid layer; 8 - outer side of reef at the "biological zero", populated by the *Cystoseira amentacea* var. *amentacea* (CYS) facies. Sampling was then carried out along a shore-sea transect, taking into account the "internal-external" hydrodynamic gradient highlighted in previous surveys (PANDOLFO *et al.*, 1992b).

Samples were washed through sieves with mesh sizes decreasing from 2mm to 0,5mm, and then sorted. After sorting and taxonomic determination to the species level, the collected *taxa* were arranged in a species/station matrix (Tab. 1). The abundance for each species in each sample was also reported as percent age dominance (Fig. 3).

A number of morphological characters (Fig. 4) for each species (RUSSO, 1989) were measured using a Wild M3Z microscope: a - shell length (sl); b - shell width (sw); c - mouth height (al); d - mouth width (aw); e - foot length (fl); f - foot width (fw).

The following morphological descriptors were then obtained from the above measurements (RUSSO, 1989): 1 - size (TG); 2 - slenderness (SL= sl/sw); 3 - spiralization (SP= sl/aw); 4 - mouth opening (AP= al/aw); 5 - shape of foot (PI= al/aw); 6 - tenacity (AD= PI/SL).

The attribution of each species to a trophic guild (CT) was based on the literature data (e.g. GRAHAM, 1988) and on the first-hand observations of the Authors. The relationships with the substratum have been inferred by *in situ* observations made by the Authors.

The progressive ranking order for each morphological descriptor (Tab. 2) was produced, based on the mean values per species (Tab. 3). The abundance and relative dominance of each single descriptor was obtained by summing the individual numbers of each species included in each rank class. Data analysis was then performed on a three-way matrix rank/sample/abundance, by the separate analysis of each single descriptor.

Factorial analysis of correspondence (FAC) was carried out on the malacofauna using a semi-quantitative species/station matrix (BENZECRI, 1976). This made it possible to arrange the taxonomic descriptors (species) along a gradient. The significance of the explained variance for each axis was tested using the FRONTIER (1974) method.

RESULTS

Twenty eight species of shelled gastropods was identified from the examination of 307 sampled specimens. The quantitative

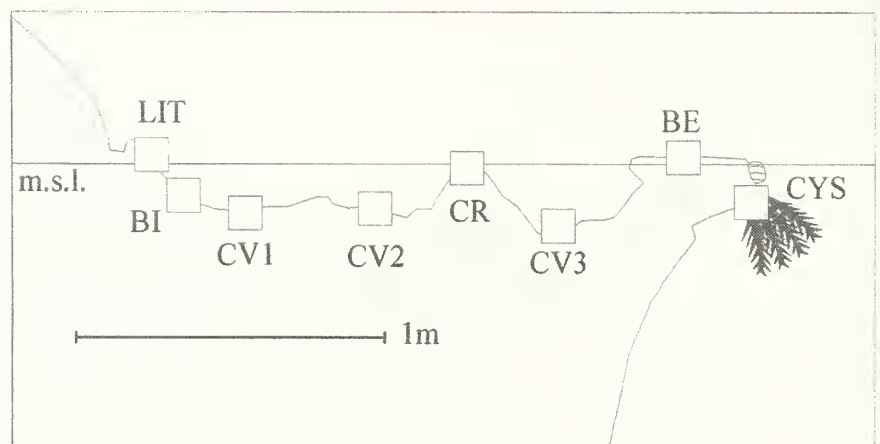


Figure 2. Scheme of the platform in cross section

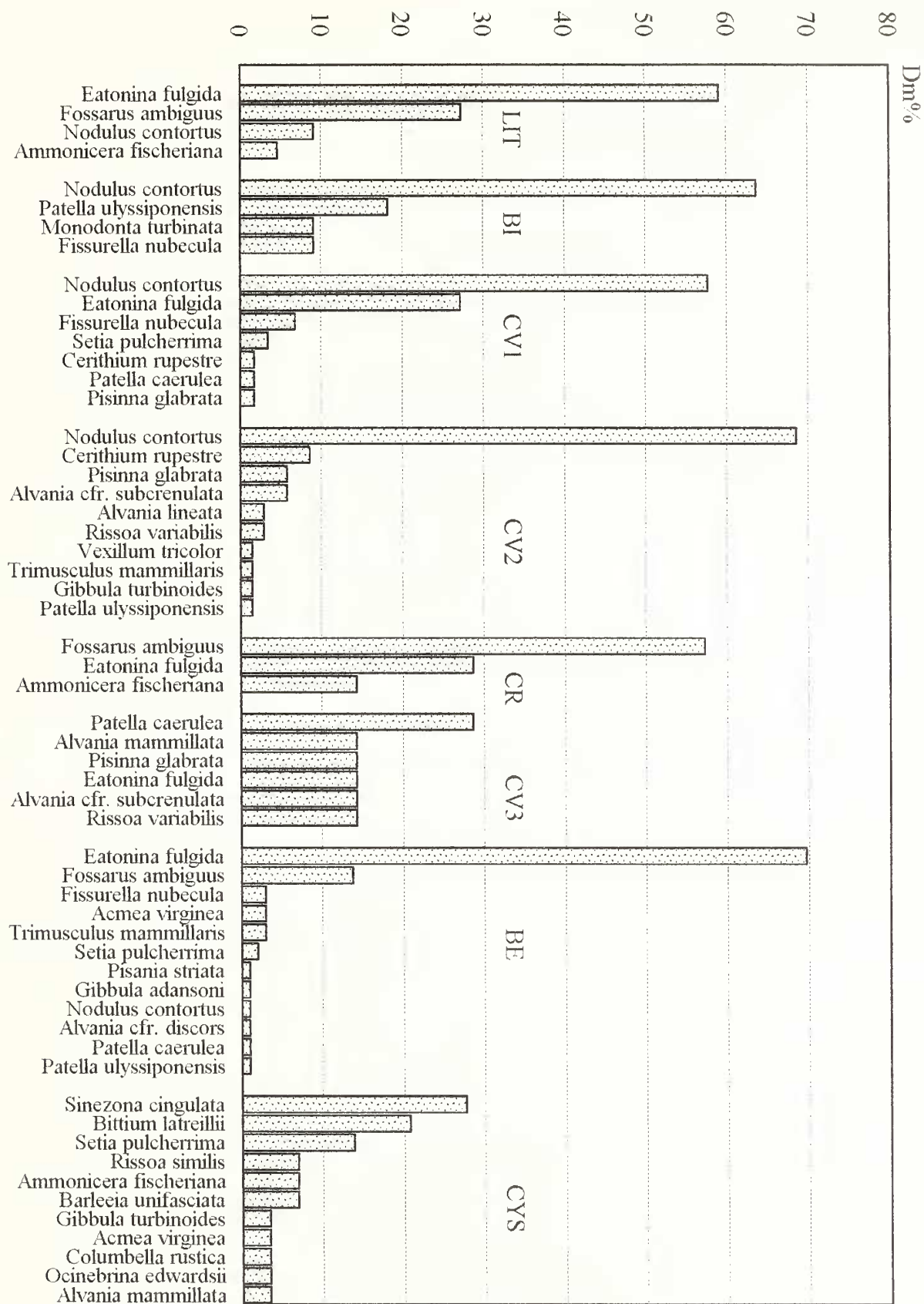


Figure 3. Percentage dominance.

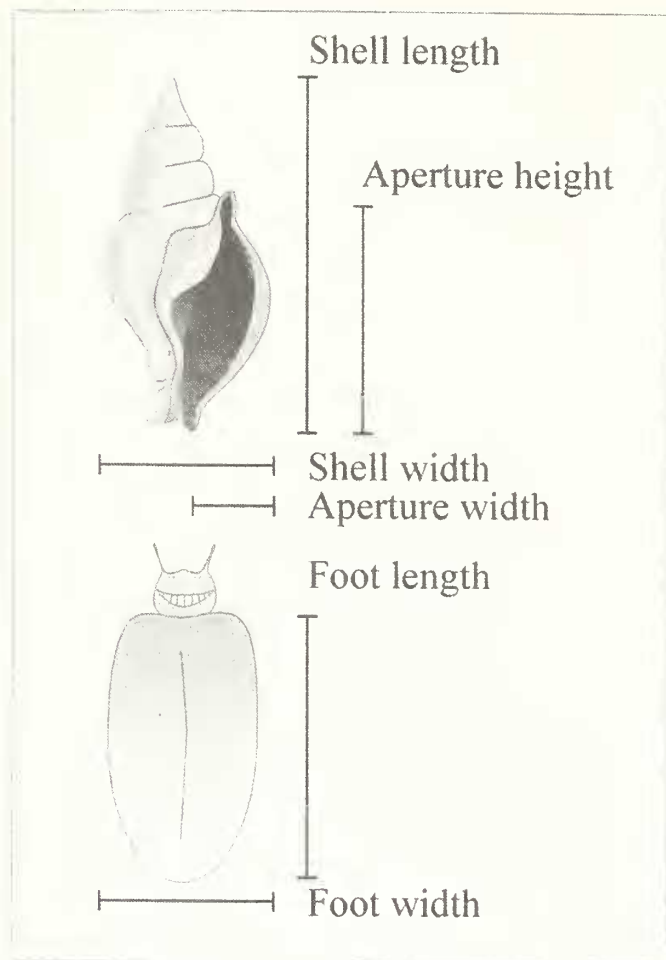


Figure 4. Measures taken on the shell and the foot.

dominance analysis for each morpho-functional descriptor produced the following results:

a) height

Five size classes were identified and arranged into ranks of increasing order (Fig. 5). Individuals of the smallest size-class (TG1) appear in all samples, with a lower frequency in CV3 and CYS, where the largest-sized individuals are more numerous. TG2 is lacking from LIT and CR, and is rare in the remaining samples, with the exclusion of BI and CV3, where it is at its maximum. TG3 is found in CV2, CV3 and in the *Cystoseira* facies. TG4 is only found in CV1 and CV2, whereas TG5 appears in BE and CYS. There is a trend of an increase in the size of the shells from the inner margin to the outer.

b) slenderness

Slenderness was divided into four decreasing classes (Fig. 6). SL1 is only found in CYS. SL2 is present in CV2, CV3 and CYS. SL3 is dominant among the classes, but its role is quite negligible in CYS, CV3 and BI, whereas SL4 is found in all samples, attaining a maximum value in BI and CYS and a minimum in LIT.

c) coiling

Three classes of coiling (Fig. 7) were plotted in decreasing order. SP1 is dominant in BI, CV1 and CV2, and is a minor component of the CV3 and CYS malacofauna. SP2 is represented in all samples, although in smaller numbers in BI and CV2, whereas it is dominant in CR. Few individuals make up SP3, which is absent from LIT and CR, while attaining its maximum in BI and CV3.

d) mouth

Among the four classes identified (Fig. 8), in decreasing order, the highest value is represented by AP1 in which the aperture is more or less circular. The frequency of AP1 is particularly low in CV2, BE and CYS, whereas AP2 characterizes only BE and CYS. AP3 and AP4 are the dominant classes along the transect.

e) foot

Foot shape was also divided into four classes (Fig. 9). The largest-foot class, PI1, appears only in CV1, CV2 and CYS. PI2 is missing from BI and increases in LIT and BE. PI3 is ubiquitous, but with lower percentages. Class PI4 is also uniformly represented in all samples.

f) tenacity

The values of the four AD classes are arranged on a low-to-high scale (Fig. 10). The lowest tenacity, AD1, is typical of CV1, CV2 and CYS, all environments with reduced wave action. AD2 is found in LIT and represented by low numbers in CV1, CV2 and BE. It is more abundant in CR and CV3 and missing from BI. Its peak is attained in CYS. AD3 is ubiquitous. AD4 is present in BI, CV1, CV3 and BE; low numbers of this class appear in CV2.

g) relationships with substratum

The relationships of the functional descriptors with the substratum were grouped into the following categories (Fig. 11):

- endolithic (ST1), i.e. organisms finding refuge in the trottoir matrix. These are typical of LIT, CR and BE;
- epilithic (ST2), living on the "trottoir" surface and collected from all samples, with a minimum in CV1 and CYS, and missing from LIT;
- epiphytic (ST3), living on benthic algae and present in all samples;
- ST4 groups species which present more than one relationship with the substratum (e.g. *Bittium latreillii*) but this category is restricted to CYS. CYS seems to represent a more diversified habitat and the same gastropod can occupy different layers of its substratum (e.g. both algae and incrustation).

h) trophic guilds

Three trophic guilds were recognized (Fig. 12): algal grazers (BRV); detritus feeders (DET) and carnivores (CAR). The BRV, feeding both on diatoms and/or on macroalgae, are the more represented along the transect. The DET appear in all samples, although in small numbers; whereas the CAR are a non-negligible component of the CYS sample. This last group includes



sponge-eating species (*Vexillum tricolor*) and predators of polychaetes (such as *Pisania striata* and *Columbella rustica*) and small bivalves like *Ocenebrina edwardsii* that feed on *Mytilaster minimus*.

FCA

Three clusters along the first two axes (F1=36.8% and F2=32.1% of the total explained variance) are evident from FCA (Fig. 13), arranged at the tips of a triangle (FRESI & GAMBI, 1982). This figure shows strong polarization due to the presence of the CYS sample, which probably belongs to the different system of the infralittoral fringe. On the other, all the remaining samples belong to an intertidal system.

The first cluster includes only the CYS sample, which included the following species: *Sinezona cingulata*, *Bittium latreilii*, *Rissoa similis*, *Barleeia unifasciata*, *Ocenebrina edwardsii* and *Columbella rustica*. CR, LIT and BE are grouped in the second cluster, with the following 5 associated species: *Gibbula adansonii*, *Fossarus ambiguus*, *Eatonina fulgida*, *Alvania discors* and *Ammonicera fischeriana*. The remaining stations, i.e. CV1, CV2, CV3 and BI are represented in the third cluster, with which are associated: *Patella ulyssiponensis*, *Monodonta turbinata*, *Cerithium rupestre*, *Rissoa similis*, *Alvania lineata*, *Alvania* cfr. *subcrenulata*, *Nodulus contortus*, *Pisina glabrata* and *Trimusculus mammillaris*.

These three clusters identify two major gradients. The first gradient refers to the F1 axis and is due to a marked separation between all the samples on the horizontal platform and the *Cystoseira* sample. This can be explained as the "midlittoral Æ infralittoral" factor. The F2 axis intercepts an "emersion / immersion" factor due to the relative position of each sample with respect to average sea level.

DISCUSSION

The spectrum of dominance of each single descriptor highlights the major role of small-sized gastropods in the entire habitat. Calcareous algae such as *Neogoniolithon notarisii* (MANNINO, 1992), small crevices and empty vermetid shells are very likely to act as refuges for this fauna, and thus ensure a higher survival rate during the frequent and long-lasting periods of desiccation

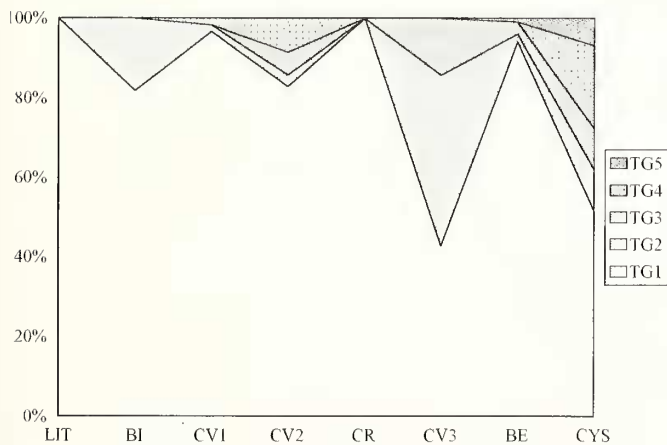


Figure 5. Distribution of height ranks.

Rank: HEIGHT	TG1<3mm 3<TG2<6mm 6<TG3<9mm 9<TG4<12mm TG5>12mm
Rank: SLENDERNESS =SL/SW	SL1>3,5 2,5<SL2<3,5 1,5<SL3<2,5 0<SL4<1,5
Rank: COILING =SL/AW	SP1>3 1<SP2<3 SP3<1
Rank: MOUTH =AL/AW	AP1>2 1,6<AP2<2 1,2 <AP3<1,6 0,8<AP4<1,2
Rank: FOOT =FL/FW	PI1>4 3<PI2<4 2<PI3<3 1<PI4<2

Table 2. Division in classes for each rank.

of the platform, which occur especially during the spring and autumn syzygial tides.

Taxa with higher TG, AP, PI and SL values are restricted to the "cuvettes" (pools) and the *Cystoseira* fringe. The relatively low hydrodynamism at the bottom of the "cuvettes" very probably has a stabilizing effect on the habitat, whereas the network of branches and leaflets of the thick *Cystoseira amentacea* stands effectively dissipates high wave energy, thereby contributing to the creation of a shelter zone during storms.

The elongated foot shape, which affords less contact the bottom, should account for the lack in CR and BE of low-tenacity taxa, which are unable to withstand wave action; the reverse is true regarding the presence of highly adhesive (AD4) species at BI and BE. AD4 species, namely *Patella ulyssiponensis* and *Patella caerulea*, are also found in the "cuvettes", due to their optimal tenacity to the substratum.

Intriguingly enough, the arrangement of organisms included in the ST1 class closely fits with the spatial development of the platform, in which the incrustation in CR and BE is proportionately thicker, whereas the highly irregular ground at LIT prevents a large number of opportunities for refuge and settlement. The algal assemblage dominated by *Laurencia papillosa*, distributed along the whole platform, shelters a rich epiphytic malacofauna with some Rissoacea



	LI	BI	CV1	CV2	CR	CV3	BE	CYS	Fr%	Dt%
1 <i>Patella caerulea</i>			1			2	1		38	1,3
2 <i>Patella ulyssiponensis</i>		2		1			1		38	1,3
3 <i>Acmea virginea</i>							3	1	25	1,3
4 <i>Fissurella nubecula</i>		1	4				3		38	2,6
5 <i>Sinezona cingulata</i>								8	13	2,6
6 <i>Gibbula adansonii</i> juv							1		13	0,3
7 <i>Gibbula turbinoides</i> juv				1				1	25	0,7
8 <i>Monodonta turbinata</i>		1							13	0,3
9 <i>Cerithium rupestre</i>			1	6					25	2,3
10 <i>Bittium latreillii</i>								6	13	2
11 <i>Fossarus ambiguus</i>	6				4		14		38	7,8
12 <i>Eatonina fulgida</i>	13		16		2	1	71		63	34
13 <i>Rissoa similis</i>								2	13	0,7
14 <i>Rissoa variabilis</i>				2		1			25	1
15 <i>Alvania lineata</i>				2					13	0,7
16 <i>Alvania mammillata</i>						1		1	25	0,7
17 <i>Alvania</i> cfr <i>discors</i>							1		13	0,3
18 <i>Alvania</i> cfr <i>subcrenulata</i>				4		1			25	1,6
19 <i>Setia pulcherrima</i>			2				2	4	38	2,6
20 <i>Nodulus contortus</i>	2	7	34	48			1		63	30
21 <i>Pisinna glabrata</i>			1	4		1			38	2
22 <i>Barleeia unifasciata</i>								2	13	0,7
23 <i>Ocinebrina edwardsii</i>								1	13	0,3
24 <i>Pisania striata</i>							1		13	0,3
25 <i>Columbella rustica</i>								1	13	0,3
26 <i>Vexillum tricolor</i>				1					13	0,3
27 <i>Ammonicera fischeriana</i>	1				1			2	38	1,3
28 <i>Trimusculus mammillaris</i>				1			3		25	1,3
Number of species	4	4	7	10	3	6	12	11		
Number of individuals	22	11	59	70	7	7	102	29		

Table 1. Species/station matrix.

such as *Eatonina fulgida*, *Nodulus contortus* and *Pisinna glabrata*.

The distribution of detritivorous species can be explained by the presence of small detritus pools represented, again, by empty shells and microcavities in the platform. The only record of carnivorous species on the *Cystoseira amnetacea* belt is due to the high degree of habitat complexity that enhances the presence of such sessile organisms as sponges, hydroids and bivalves which are the favourite prey items of carnivorous gastropods.

The total set of gastropod species making up the "trottoir à vermetes" taxocoene can be thought of as composed of the following 4 leading morphogroups (Fig. 14) (CIUNA *et al.*, 1995),

which have no real taxonomic significance, and are similar to those indicated by MOORE (1960):

1. **patelloid**, with morphological parameters like those of *Patella* and *Acmaea*, i.e.: short shell, low slenderness and high tenacity due to a large, round foot;
2. **trochoid**, resembling to *Monodonta* or *Gibbula*, with medium height, medium slenderness and high tenacity;
3. **rissoid**, in according with the data obtained from *Rissoa* or *Pisinna*, with low or medium height, high slenderness and low tenacity;
4. **muricoid**, with parameters like those of *Pisania* or *Muricopsis* i.e. very high shell, high slenderness and low tenacity.



		TG	SL	SP	AP	PI	AD	ST	CT
1	<i>Patella caerulea</i>	2	4	4	3	4	4	2	BrV
2	<i>Patella ulyssiponensis</i>	2	4	4	3	4	4	2	BrV
3	<i>Acmea virginea</i>	1	4	4	2	4	4	1	BrV
4	<i>Fissurella nubecula</i>	1	4	4	3	3	4	2	BrV
5	<i>Sinezona cingulata</i>	1	4	3	4	4	2	3	Det
6	<i>Gibbula adansonii</i>	1	4	3	4	4	3	3	BrV
7	<i>Gibbula turbinoides</i> juv.	3	4	3	4	4	3	3	BrV
8	<i>Monodonta turbinata</i> juv.	1	4	3	4	4	3	2	BrV
9	<i>Cerithium rupestre</i>	4	3	1	3	1	1	2	Det
10	<i>Bittium latreillii</i>	4	1	1	2	1	1	4	Det
11	<i>Fossarus ambiguus</i>	1	3	3	4	3	3	1	Det
12	<i>Eatonina fulgida</i>	1	3	2	3	2	3	3	Det
13	<i>Rissoa similis</i>	3	2	1	3	3	3	3	Det
14	<i>Rissoa variabilis</i>	3	2	1	3	3	3	3	Det
15	<i>Alvania lineata</i>	1	4	2	3	2	2	3	Det
16	<i>Alvania mammillata</i>	2	3	2	3	2	2	3	Det
17	<i>Alvania</i> cfr <i>discors</i>	1	3	2	3	2	2	3	Det
18	<i>Alvania</i> cfr <i>subcrenulata</i>	1	3	2	3	2	2	2	Det
19	<i>Setia pulcherrima</i>	1	3	2	3	2	2	3	Det
20	<i>Nodulus contortus</i>	1	3	1	4	4	3	3	Det
21	<i>Pisinna glabrata</i>	1	3	1	4	4	3	3	Det
22	<i>Barleeia unifasciata</i>	2	3	1	4	3	3	3	Det
23	<i>Ocenebrina edwardsii</i>	5	3	1	1	3	2	2	Car
24	<i>Pisania striata</i>	5	3	2	1	3	2	2	Car
25	<i>Columbella rustica</i>	5	3	1	1	3	2	3	Car
26	<i>Vexillum tricolor</i>	2	2	1	1	3	2	2	Car
27	<i>Ammonicera fischeriana</i>	1	4	3	4	4	2	3	BrV
28	<i>Trimusculus mammillaris</i>	3	4	4	3	4	4	2	BrV

Table 3. Classification in rank for each species.

Finally, Fig. 15 shows the distribution patterns of the above morphological groups along the platform, which closely agree with the capacity of the species to sense the environmental parameters, above all the hydrodynamic pattern. This pattern can be modelled (Fig. 16) using the distribution of the morphogroups as descriptors of the average hydrodynamic conditions along the platform. Obviously this "indirect" model could be considered descriptive only of the environmental conditions during the sampling. A more accurate study will be performed combining two seasons of sampling (summer and winter).

CONCLUSION

From this survey, the gastropod taxocoene alone can be deemed an exhaustive and quite satisfactory descriptor of the gradient examined. Moreover, the information provided by this *syntaxon*

are in close agreement with the conclusions from previous research (PANDOLFO *et al.*, 1992a; 1992b).

Three groups of species are highlighted: the first is related to the *Cystoseira amentacea* belt, and can be considered as belonging to the true infralittoral; a second group is restricted to the highest portions of the platform (midlittoral species-group) and a third one is restricted to the tide-pools and crevices inside the reef (infralittoral species-group). These species belong to four different morphogroups which are distributed differently along the platform, reflecting their hydrodynamic tolerance.

One conclusion of the above discussion is that there exist at least two distinct conditions in the same environment which are responsible for the diversity of the faunistic assemblages: one can be deemed as an emersion condition and is related to the vermetid crests and protruding edges which emerge above the

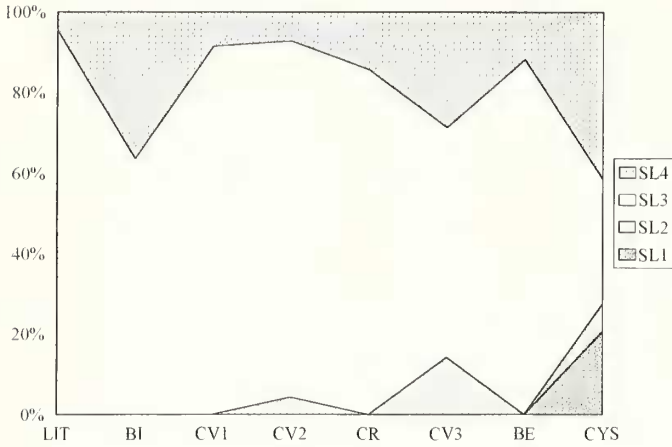


Figure 6. Distribution of slenderness ranks.

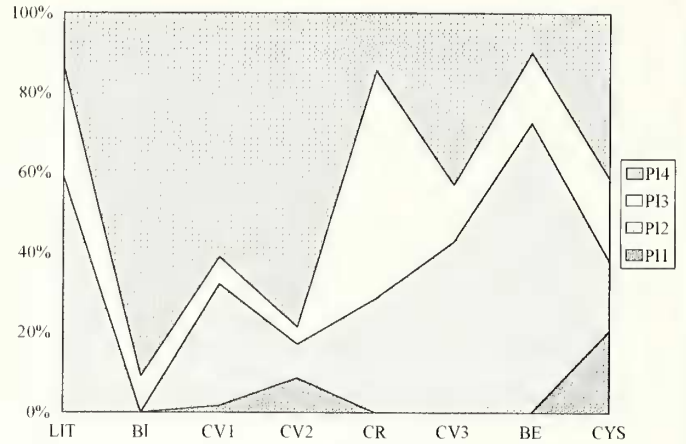


Figure 9. Distribution of foot shapes.

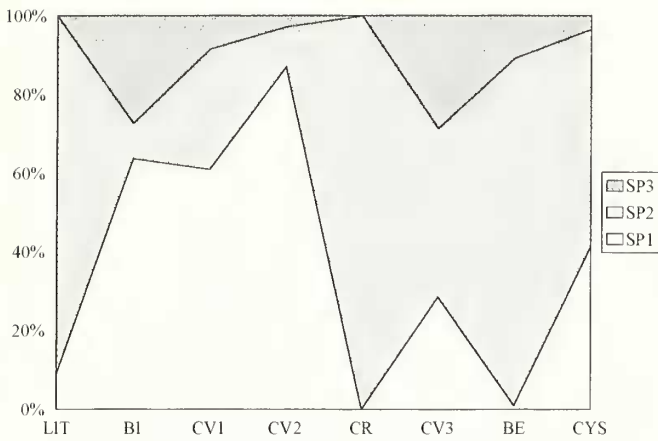


Figure 7. Distribution of coiling ranks.

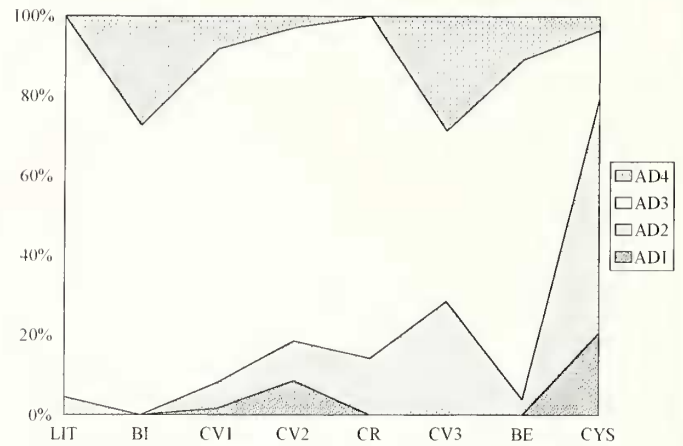


Figure 10. Distribution of tenacity.

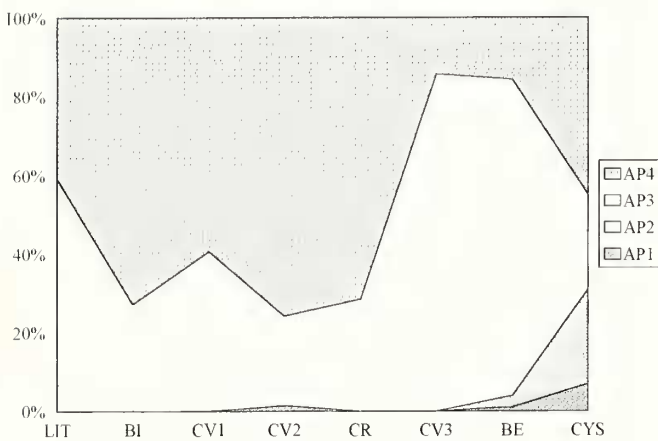


Figure 8. Distribution of aperture shapes.

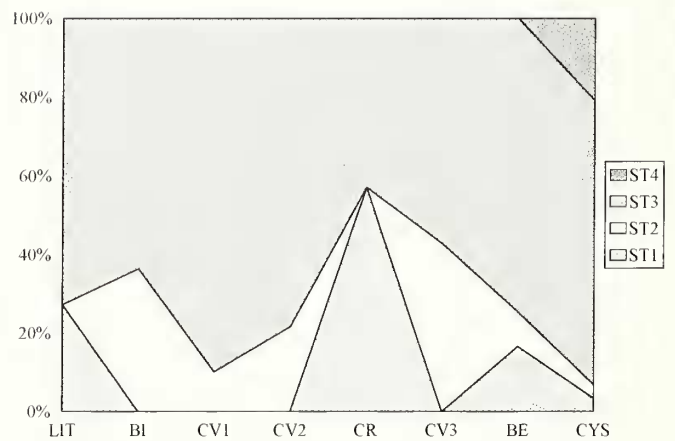


Figure 11. Distribution according to the relationships with substratum.

tide level and therefore endure more or less long intervals of complete drought. The second condition is related to those portions of the platform continuously submerged or lined with a thin film of water. The transition between these two extremes, complicated by the wave action, can be seen as the hydrodynamic gradient highlighted by the distribution cluster of FAC.

The identification of an "emersion-immersion" factor along

the vermetid platform is the major finding of our survey. Such a finding gives new insight in the understanding of the role and spatial distribution of the platform's biotic components, and aids the designing of a new dynamic model of this habitat. This model indicates the coexistence of at least two distinct zones in a restricted space, distinguished by the prevalence of hydrodynamic factors.

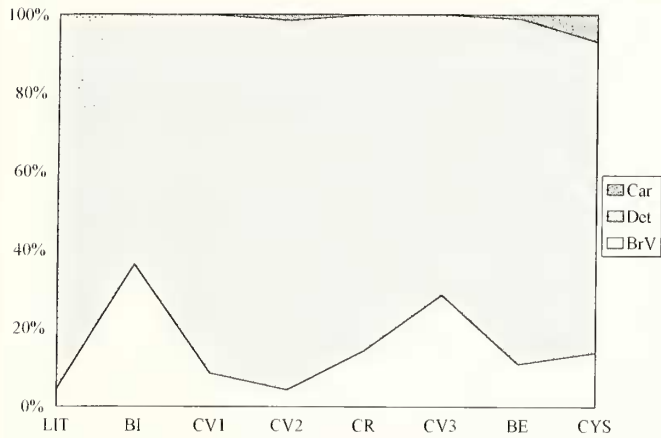


Figure 12. Distribution of the trophic guilds.

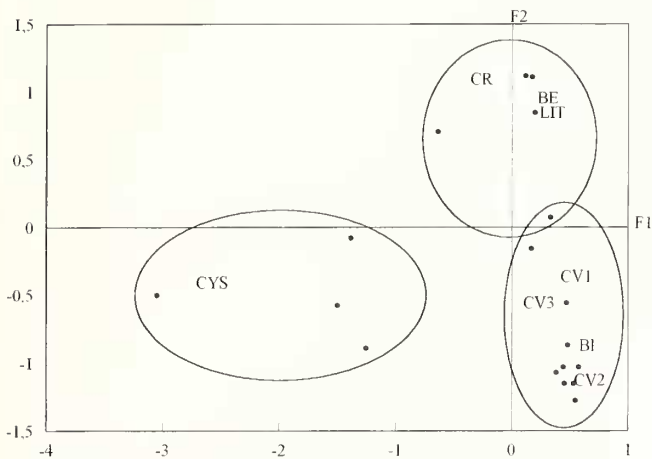


Figure 13. Factorial analysis of correspondence on raw data.

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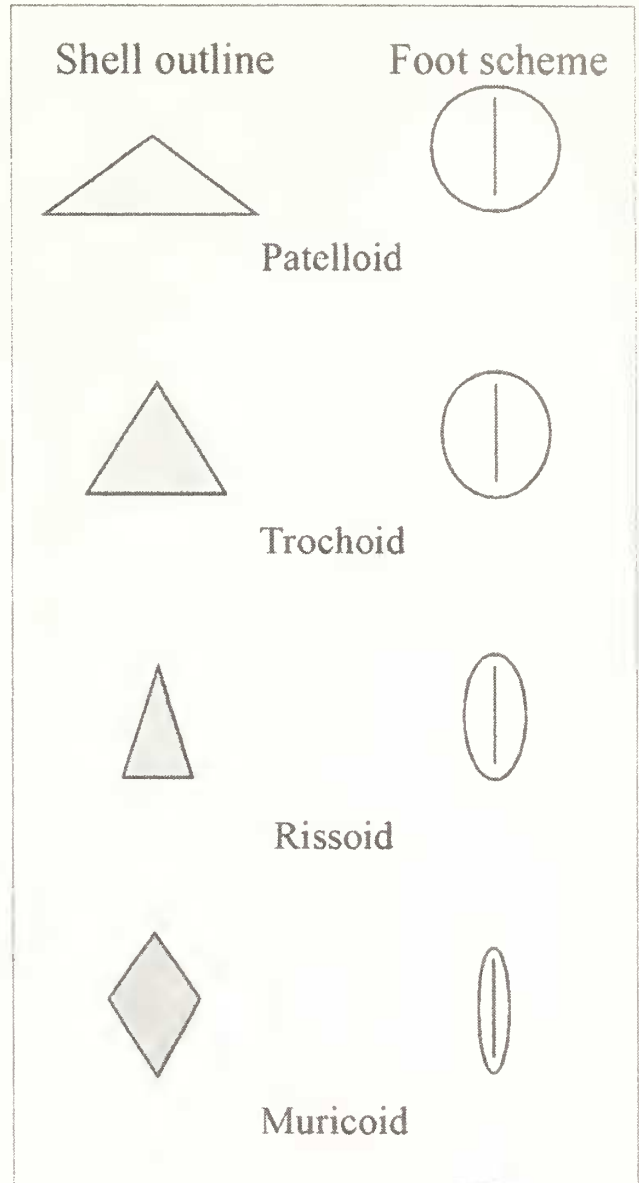


Figure 14. Morphogroups.

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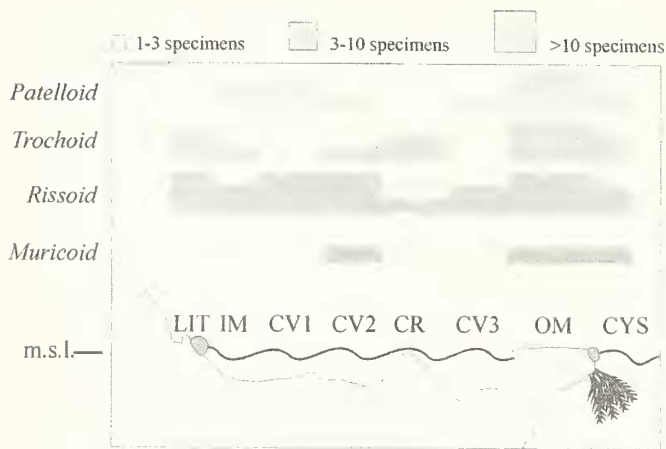


Figure 15. Distribution of morphogroups along the platform.

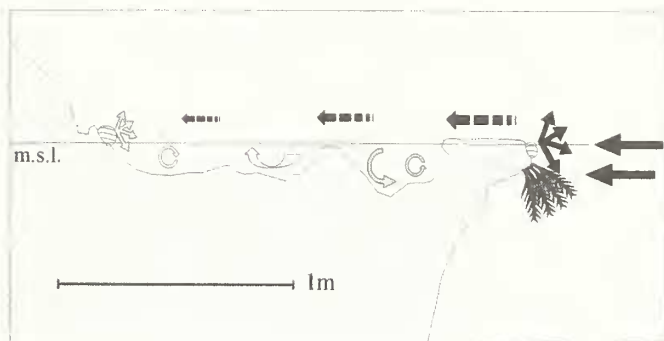


Figure 16. Hydrological model.

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